

DISTRIBUTION AND ECOLOGY OF *HYDRAENA*
KUGELANN IN THE NETHERLANDS (COLEOPTERA:
HYDRAENIDAE)

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The distribution patterns of the species of the genus *Hydraena* in The Netherlands are figured. Their habitats are briefly described and compared with references. Physical/chemical data, phenologies and co-existence of species, based on observations by the author, are presented.

Hydraena species mainly living in stagnant waters have relatively wide distributional areas in The Netherlands. *Hydraena* species from running waters are confined to the most eastern and southern part of the country and some of them may have disappeared at the beginning of this century. Chlorinity explains best the different distribution patterns of the stagnant water *Hydraena*. All stagnant water species can co-exist and their phenology is more or less the same with a high (early) spring maximum and most often a (lower) autumn maximum, indicating an univoltine life cycle.

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Key words. – *Hydraena*; distribution maps; ecology; co-existence; The Netherlands.

Beetles of the genus *Hydraena* Kugelann are small water beetles (1.5-2.5 mm) characterised by parallel sides, club-shaped antennae and very long maxillary palps. Sexes can be distinguished easily as males have six visible abdominal sternites, while females have seven. Many species show secondary sexual differences, which sometimes offer useful characters for the identification of the species. Many species, however, can only be reliably identified in the male sex by their genitalia. In the past the study of genitalia has been neglected in The Netherlands owing to the lack of illustrated (Dutch) keys and by the former practice of relying entirely on external characters. An illustrated key to the Dutch species is now available (Cuppen 1992) to which one is referred for identification.

The present survey is the first covering all species of *Hydraena* in The Netherlands and gives distribution maps based on old records, which have been checked in relation with taxonomic uncertainties, and recently collected material. A survey of phenology and ecology is presented on the basis of literature and own field-work on mainly the stagnant water *Hydraena*.

MATERIAL AND METHODS

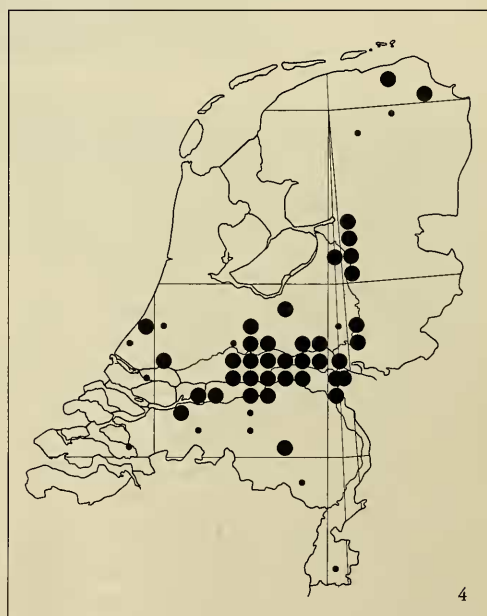
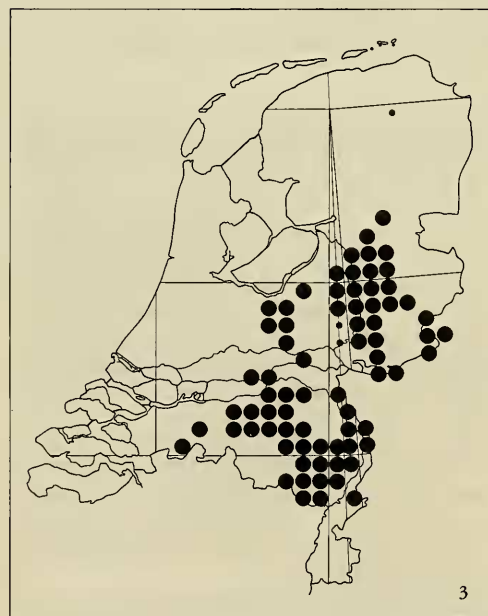
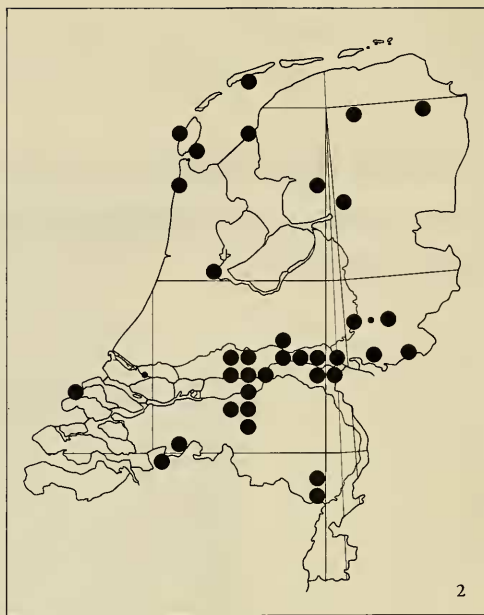
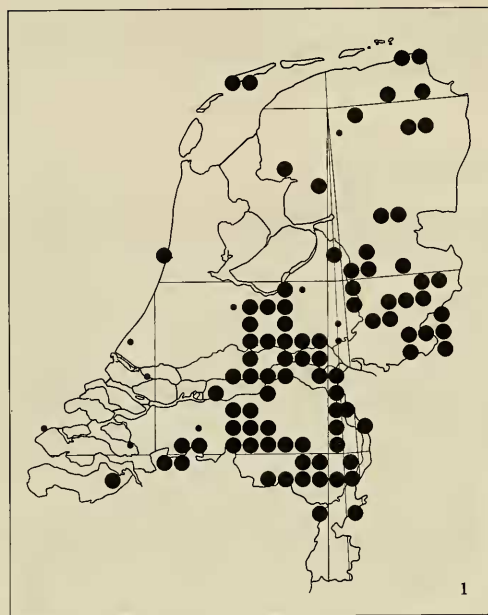
The material of this study includes the collections

of the National Museum of Natural History, Leiden (RMNH), the Zoological Museum, Amsterdam (ZMA), the Departments of Entomology and Nature Conservation of the Wageningen Agricultural University, and the private collections of H. Cuppen (Apeldoorn), B. Drost (Wadenoyen), G. van Ee (Haarlem), J. Huijbregts (Leidschendam), B. van Maanen (Wageningen), H. Vallenduuk (Boxtel), C. Visser (Wageningen), B. van Vondel (Hendrik-Ido-Ambacht), O. Vorst (Utrecht) and the author. Some data from the Provincial Water Authorities of Noord-Holland and Utrecht, and from the Research Institute for Nature Management are also included. The maps are based on specimens, identified by the author. For *Hydraena riparia* Kugelann, *Hydraena assimilis* Rey and *H. melas* Dalla Torre in the *H. riparia*-complex (see Jäch 1988), the maps are based on records of males only.

The distribution of the *Hydraena* species in The Netherlands is plotted in the 10 km-squares of the UTM-grid (figs. 1-12) in which small dots refer to records before 1950 and large dots to records since 1950.

On most localities visited by the author a water sample has been taken, which has been analysed the same or the next day on pH, electrical conductivity, chlorinity and total hardness. The results, viz. the ranges, 90% ranges and median values are presented in tables 1-4.

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Figs. 1-4. Distribution of *Hydraena* species in the Netherlands. – 1, *Hydraena testacea* Curtis; 2, *Hydraena palustris* Erichson; 3, *Hydraena britteni* Joy; 4, *Hydraena riparia* Kugelann (males only).

Data on phenology and ecology are mainly based on the author's observations from The Netherlands and are compared with data from literature. Owing to the paucity of records for most species, statistical

treatment of ecological data was not possible. For some species only old records are available and there is little information concerning ecology as labelling was insufficient in the past.

HABITAT AND DISTRIBUTION

All Dutch *Hydraena* species are widely distributed in Europe (Ienistea 1978, Hebauer 1980, Horion 1949, Berthélemy 1986, d'Orchymont 1925, Jäch 1988). Detailed distribution maps for *Hydraena*, using any grid system, are given by Nilsson (1984) for the northern part of Sweden (50 km-squares) and Foster (1990) for the British Isles (10 km-squares).

Relatively small on an European scale are the distribution areas of *H. assimilis*, *H. melas*, *H. belgica* d'Orchymont and *H. excisa* Kiesenwetter. The Dutch localities of *H. excisa* form an extreme western outpost of this eastern European species.

Running waters including spring-fed streams are confined to the southern, central and eastern part of The Netherlands and therefore many rheophilic species of *Hydraena* are restricted to these parts of the country. Stagnant waters, however, occur all over the country. Brackish waters are mainly found in the south-western and northern part of the country (and before 1950 also around the Zuiderzee). The sandy soils in the southern, central and eastern part of the country, and the coastal dune area have usually a chlorinity of less than 100 mg/l, while the clay soils in the western and northern part have a chlorinity of more than 50 mg/l and gradually pass into the brackish areas. The main soil types per 10 km UTM grid-square are presented by Van Tol (1981).

NOTES PER SPECIES

H. testacea Curtis
(fig. 1).

This species is recorded from 89 squares since 1950 and additionally from 10 squares before 1950. It is the commonest species of the genus *Hydraena* in The Netherlands, collected mainly in the northern, eastern and southern part of the country. From the western part of the country there is only one recent record, apart from some pre 1950 records, despite large sampling programmes in recent years. The lack of records from Flevoland is probably due to under-sampling. South-Limburg apparently has no proper habitats for this species.

Most records of *H. testacea* in the present investigation are from temporary, semi-permanent and permanent stagnant waters with a well developed marginal vegetation dominated by *Carex*, *Glyceria maxima* (Hartman) Holmberg, *Phragmites australis* (Cav.) Steudel, *Calamagrostis canescens* (Weber) Roth or *Juncus effusus* L. Certainly the marginal vegetation is not a necessity as the species was frequently found in waters without any marginal vegetation or with only a submerged vegetation. Also, in slowly running wa-

ters such as regulated streams, *H. testacea* occurs frequently. In fast running waters the species is extremely rare in The Netherlands. This species is generally mentioned from stagnant waters, often with a well developed marginal vegetation as well as slowly running waters (d'Orchymont 1925; Horion 1949; Hrbáček 1951; Balfour-Browne 1958). Derenne (1952) mentions its occurrence in slowly running waters dominated by algae. The occurrence in fast running waters is only mentioned by Cuppen (1985) and Horion (1949) in *Fontinalis* in clear mountain-brooks. The habitat investigations by the author fairly well agree with literature for this species.

H. palustris Erichson
(fig. 2).

This is an uncommon species recorded from 35 squares since 1950 and additionally from two squares before 1950. The general distribution pattern of *H. palustris* resembles that of *H. testacea*, but with much larger gaps and some isolated populations in the coastal dune area. The only area with a more or less continuous cover of squares is formed by the fresh water part of the river district.

With one exception (in a regulated stream), all Dutch records of *H. palustris* are from temporary, semi-permanent and permanent stagnant waters. The species prefers temporary and semi-permanent, overgrown ditches and pools with *Carex*, *Phragmites australis*, *Phalaris arundinacea* L., *Calamagrostis canescens* and *Glyceria maxima*, in which the soil is covered by organic debris of the dominant plants. Most localities are unshaded or only partly shaded by *Salix*. In permanent ponds, ditches and canals *H. palustris* has been found only where a well developed marginal vegetation of helophytes is present. Generally *H. palustris* is considered to be a species of stagnant waters (d'Orchymont 1925; Derenne 1952), which are covered by aquatic macrophytes (Horion 1949; Hebauer 1980) or mosses (Balfour-Browne 1958) as forest-pools, fens, ponds and ditches. The rare occurrence in running water is only mentioned by Horion (1949) and Hebauer (1980). Hebauer (1980) mentions a preference for acid waters, which could not be confirmed in the present investigations.

H. britteni Joy
(fig. 3).

This species was recorded from The Netherlands from 18 squares in 1982 by Cuppen & Cuppen. At present this rather common species is known from 73 squares since 1950 and additionally from three squares before 1950. The low number of specimens in museum collections in comparison with other *Hydraena* species is very remarkable. The large increase of the number of records is caused by specific

sampling in autumn, winter and early spring. *H. britteni* is confined to the southern and eastern part of the country with one old record from the province of Groningen (Haren; coll. ZMA). *H. britteni* fails in South-Limburg and occurs locally in the river area behind dikes of the rivers Rhine and Waal (Drost 1989). Records of *H. nigrita* by Everts (1898; 1922) belong to this species.

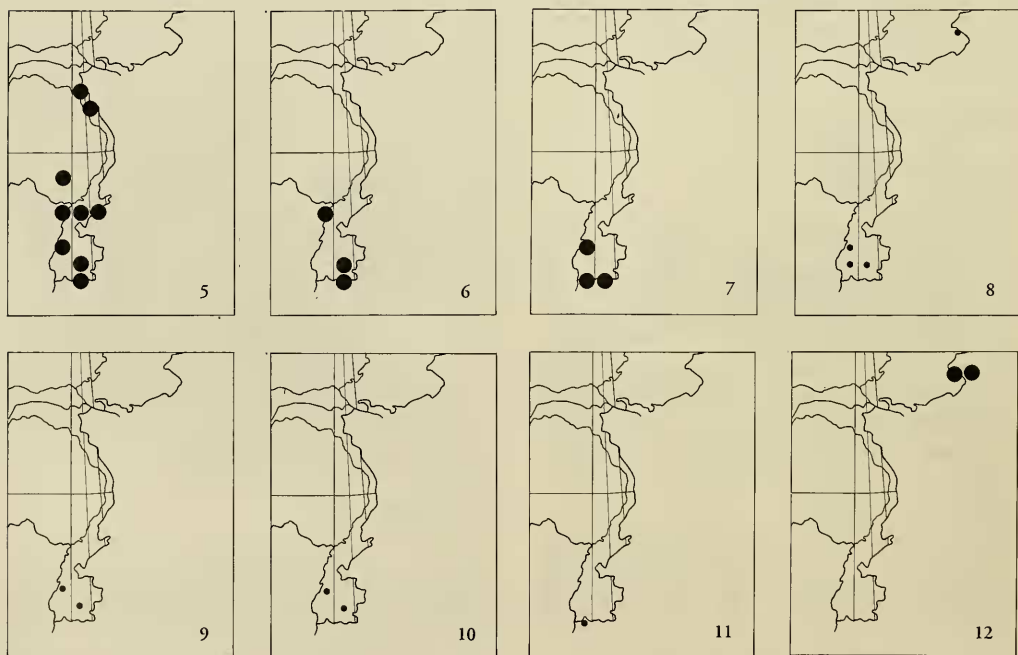
H. britteni is considered to inhabit smaller stagnant waters, such as vegetation-rich pools and ditches, often rich in mosses or with decaying leaves (Hrbáček 1951; Derenne 1952; Hebauer 1980; Nilsson 1984). Dutch habitats of *H. britteni* are characterized by Cuppen & Cuppen (1982) as temporary, weakly acid, stagnant waters with peaty soils covered by coarse organic debris. Such habitats are alder-brooks, forest-drains and -pools, marshes and swampy ditches dominated by *Phragmites australis*, *Phalaris arundinacea*, *Calamagrostis canescens*, *Glyceria maxima* or *Carex*. The acidophilic character of the habitat of *H. britteni* mentioned by Hebauer (1980) is confirmed above. The occurrence in a variety of running waters (Hebauer 1980; Balfour-Browne 1958), especially those with grassy edges in partial shade (Foster 1990) and cold springs (Nilsson 1984) is only confirmed for

small sluggish streams receiving seepage-water. The incidental records in The Netherlands in larger streams most probably concern specimens that are washed out from their normal habitats during high water or flyers from habitats which have been dried out during the summer. There are some records of *H. britteni*, sifted from litter, in the summer period in dried out habitats (Vorst, pers. comm.). Landin (1976) mentions the presence of *H. britteni* and larvae of *Hydraena* above the water line.

H. riparia Kugelann (fig. 4).

After the splitting up of *H. riparia* and *H. assimilis* by Jäch (1988), a comparison between literature and the present data is difficult. *H. riparia* is known from 38 squares since 1950 and additionally from 13 before 1950. The map gives only records of males and the species can be considered as rather common. Most records are confined to the river area with some recent records from the northern and western part of the country, and some old records from the south.

Jäch (1988) mentions *H. riparia* from very fast flowing streams and not in stagnant waters, while Nilsson (1984) mentions exposed lakeshores among



Figs. 5-12. Distribution of *Hydraena* species in The Netherlands. – 5, *Hydraena assimilis* Rey (males only); 6, *Hydraena melas* Dalla Torre (males only); 7, *Hydraena pygmaea* Waterhouse; 8, *Hydraena pulchella* Germar; 9, *Hydraena minutissima* Stephens; 10, *Hydraena gracilis* Germar; 11, *Hydraena belgica* d'Orchymont; 12, *Hydraena excisa* Kiesenwetter.

sand and gravel in Sweden. In England Balfour-Browne (1958) records the species from both stagnant and running waters. The Dutch data contradict the findings of Jäch (1988) and Nilsson (1984): there are no records of *H. riparia* in fast flowing waters nor on exposed lake shores. The species is mainly confined to stagnant waters and is occasionally found in slowly running, small streams. In fact most records are from temporary and semi-permanent habitats with a well developed vegetation of *Phragmites australis*, *Glyceria maxima* or *Carex* and soils covered by coarse organic debris or, in the case of running waters, small shady brooklets less than one meter wide. The occurrence in larger ditches and ponds has been found only when there exists a well developed marginal vegetation or, single specimens have been found, when the appropriate habitats are within close vicinity.

H. assimilis Rey
(fig. 5).

This very rare species is recorded from 9 squares since 1950 in the south-eastern part of the country (provinces of Limburg and Gelderland), but very probably some pre-1950 females from Limburg belong to this species. The map gives only records of males.

The few Dutch records of this species originate from small ditches and pools, receiving seepage-water, with or without vegetation, and from some small, relatively fast flowing streams. The only reference (Jäch 1988) mentions the same habitats as for *H. riparia* as the most probable.

H. melas Dalla Torre
(fig. 6).

This very rare species was recorded for the first time from The Netherlands by Cuppen (1981) from Beertsenhoven. There are additional records of single males from Epen (coll. RMNH and coll. O. Vorst) and the Middelsgraaf near Echt (coll. J. Cuppen).

The few Dutch records of *H. melas* are from spring-fed, small streams and, in one case, a larger, sun-exposed, slowly running stream. The references for *H. melas* are contradictory: Hrbáček (1951) and Hebauer (1980) mention preference for cold streams in mountainous areas, as well as acid ditches with much detritus in river valleys, while Jäch (1988) mentions mainly stagnant waters and small springs, but occasionally in larger streams and rivers.

[*H. nigrita* Germar]

The specimens from Warnsveld and Breda, mentioned by Everts (1898, 1922), are deposited in the RMNH-collection and appear to belong to *H. britteni*. For this reason *H. nigrita* has to be removed from the Dutch list.

H. pygmaea Waterhouse
(fig. 7).

This very rare species is recorded from three squares since 1950 in South-Limburg (Bunde, Epen, Houthem, Noorbeek en Cottessen) with the last record from 1991.

The few recent Dutch records of *H. pygmaea* are from small (width less than 1 m), relatively fast flowing streams, which are heavily shaded in one case and unshaded in two. Generally this species is confined to running waters in hills and mountains (Horion 1949; Hrbáček 1951; Derenne 1952; Balfour-Browne 1958). Apparently *H. pygmaea* prefers sites with aquatic mosses and periphyton on wires and boulders (Hebauer 1980, Foster 1990). Hebauer (1980) refers to the species as cold-stenotherm and crenophilic, confined to the upper courses of streams and rarely found in the middle course. The Dutch data confirm the restriction of *H. pygmaea* to the smallest streams.

H. pulchella Germar
(fig. 8).

Forty specimens of this very rare species were taken in four squares in South-Limburg and the vicinity of Winterswijk, all at the end of the 19th century or the beginning of the 20th century. A large series from 1921 (Wylre) represents the last record. *H. pulchella* is regarded to be extinct in The Netherlands.

The Dutch records of *H. pulchella* suggest that, in the past, this species mainly occurred in the larger, fast-flowing streams (rivers Geul, Gulp and Ratumse Beek). Generally *H. pulchella* is confined to running waters, especially mossy stones and grassy edges (Hrbáček 1951; Derenne 1952; Balfour-Browne 1958; Hebauer 1980). Foster (1990) mentions exposed muddy pools in a small stream with riffles and pools, and amongst fine tree roots in a clayey gorge in a river. In comparison with *H. pygmaea*, this species is more restricted to middle courses and open, exposed parts of a stream. Hebauer (1980) refers to it as a rheobiontic, eurythermous species.

H. minutissima Stephens
(fig. 9).

This very rare species is only known from two squares with 15 specimens altogether. The last record is from 1920 (Gulpen) and the species is regarded to be extinct in The Netherlands.

The few (old) records from The Netherlands probably all originate from the middle courses of the Geul and the Gulp, which are relatively fast flowing streams. Abroad this running water species has been found in small and large streams between gravel and aquatic mosses (Hrbáček 1951; Derenne 1952; Balfour-Browne 1958; Hebauer 1980; Valladares

1989). The distribution of *H. minutissima* seems to depend on strong current, rather than on temperature-regime (Hebauer 1980).

H. gracilis Germar
(fig. 10)

There are only three specimens from two squares known from The Netherlands. A record from 1923 (coll. ZMA) is the last and the species is regarded to be extinct in The Netherlands. Most records of this species by Everts (1898, 1922) appear to belong to either *H. belgica* or *H. excisa*.

Generally *H. gracilis* is considered to be the most common running water *Hydraena* in western and central Europe, which occurs from the upper course till the lower course, as well in cold as in exposed streams and as well in mountains as on plains (Pretner 1930, Hebauer 1980, Valladares 1989). Also, with reference to the current velocity, the species shows a wide amplitude as Derenne (1952) even mentions stagnant waters. In these habitats the species can be found in mosses, under stones and in gravel (Horion 1949, Balfour-Browne 1958, Nilsson 1984). Despite this wide ecological amplitude *H. gracilis* has only been found twice in probably the middle and lower course of the Geul.

H. belgica d'Orchymont
(fig. 11)

The only Dutch record is from the middle course of the Voer river (width of 3-5 m), probably from the beginning of the 20th century (coll. RMNH). No further details are known. *H. belgica* most probably no longer occurs in The Netherlands. Everts (1922) refers to these specimens as *H. gracilis*.

The habitat of *H. belgica* in The Netherlands corresponds with Derenne (1952), who simply refers to streams as its habitat. Hrbáček (1951) mentions small (shady) streams with a moderate slope.

H. excisa Kiesenwetter
(fig. 12).

This very rare species is known from only two

squares since 1950 in the vicinity of Winterswijk. Tolkamp (1980) lists *H. excisa* for the first time for The Netherlands, without mentioning it as an addition to the Dutch fauna. However, Everts (1898) already recorded *H. gracilis* var. *erosa* and var. *excisa* from Winterswijk, but the material could not be found in the museum collections. The first specimens from Winterswijk, labelled as *H. gracilis*, in these collections date from 1918 and all later references (Everts 1922, Lajendecker & Nieser 1971) belong to *H. excisa*.

The recent Dutch records are from the Ratumse Beek (width about 3-5 m with shaded and unshaded sections) and some smaller tributaries. The species has been found here amongst gravel in relatively fast flowing parts of the stream (Lajendecker & Nieser 1971, Tolkamp 1980). Elsewhere in Europe *H. excisa* occurs in small, shady streams with a moderate slope (Hrbáček 1951) or sun-exposed streams (Hebauer 1980). According to the latter author the species is not cold-stenotherm and has no preference with respect to calcium. Within the streams it can be found in mosses or between and under stones (Knie 1974; Hebauer 1980).

PHYSICAL AND CHEMICAL DATA

The ranges of the observed pH-values (table 1) are large for most *Hydraena* species. However, the median values of pH for all frequently encountered *Hydraena* species are between 6.5 and 7.0, with 90% of the observed values within 1.3 pH-unit above or below the median pH of that species. *H. britteni* has the lowest median pH-value and *H. riparia* the highest. As the 90% ranges of pH for the different species considerably overlap and the median values are very close to each other, the pH can not be considered a very important factor for the explanation of the different geographic distribution patterns of these *Hydraena* species in The Netherlands.

Ranges for the values of the electrical conductivity (table 2) are very large for *H. riparia* and *H. testacea* and large for *H. britteni* and *H. palustris*. The 90% ranges for the most common species reduce the upper limit for electrical conductivity considerably with the smallest range for *H. britteni* and a larger, more or less the same, range for the other species. The median value of electrical conductivity is distinctly higher for *H. riparia* in comparison with the other species, which partly can be explained by the different distribution patterns of these species. However, also in this respect there is a considerable overlap in ranges.

Ranges, 90% ranges and median values of total hardness (table 3) are more or less the same for the common *Hydraena* species and certainly cannot explain their different geographic distribution patterns.

Table 1. Range, 90% range and median of observed pH-values on localities of *Hydraena* species in The Netherlands. N is the number of observations.

	range	90% range	median	N
<i>Hydraena assimilis</i>	6.3 - 9.0		6.8	6
<i>Hydraena britteni</i>	4.7 - 7.8	5.5 - 7.3	6.5	88
<i>Hydraena melas</i>	7.1 - 9.0			2
<i>Hydraena palustris</i>	3.5 - 9.2	5.3 - 7.7	6.8	45
<i>Hydraena pygmaea</i>	7.9			1
<i>Hydraena riparia</i>	3.3 - 8.3	6.2 - 7.8	7.0	174
<i>Hydraena testacea</i>	3.5 - 9.9	5.5 - 8.0	6.8	151

Table 2. Range, 90% range and median of observed values of electrical conductivity ($\mu\text{S cm}^{-1}$) on localities of *Hydraena* species in The Netherlands. N is the number of observations.

	range	90% range	median	N
<i>Hydraena assimilis</i>	330 - 710		490	6
<i>Hydraena britteni</i>	107 - 1260	192 - 730	450	88
<i>Hydraena melas</i>	420 - 620			2
<i>Hydraena palustris</i>	124 - 1590	150 - 1030	440	45
<i>Hydraena pygmaea</i>	580			1
<i>Hydraena riparia</i>	55 - 2030	228 - 1140	560	174
<i>Hydraena testacea</i>	87 - 2030	174 - 1030	460	151

Table 3. Range, 90% range and median of observed values for total hardness (°D) on localities of *Hydraena* species in The Netherlands. N is the number of observations.

	range	90% range	median	N
<i>Hydraena assimilis</i>	6 - 14		10	6
<i>Hydraena britteni</i>	1 - 23	3 - 16	8	46
<i>Hydraena melas</i>	9			1
<i>Hydraena palustris</i>	2 - 25	3 - 21	6	33
<i>Hydraena riparia</i>	1 - 26	4 - 21	9	77
<i>Hydraena testacea</i>	1 - 25	2 - 16	6	88

Based on only 6 observations, *H. assimilis* has a relatively small range with a high median value.

Of the four investigated parameters, chlorinity is the most informative with respect to the distribution patterns of *Hydraena* (table 4). All species are confined to fresh water with only one sample with a chlorinity of more than 200 mg/l for *H. britteni*, *H. palustris* and *H. testacea*, while for *H. riparia* there are five. Chlorinity is certainly highly responsible for the absence of *Hydraena* species in the western and northern part of the country of which the coastal dune area is excluded due to the presence of fresh waters. Median and 90% ranges of the most common *Hydraena* species are also in agreement with their general distribution patterns: *H. riparia* occurs mainly between the large river systems, *H. palustris* is scattered all over the country with the exception of brackish parts, *H. testacea* occurs on sandy soils in the

Table 4. Range, 90% range and median of Cl--values (mg l^{-1}) on localities of *Hydraena* species in The Netherlands. N is the number of observations.

	range	90% range	median	N
<i>Hydraena assimilis</i>	36.5 - 102.8		41.9	6
<i>Hydraena britteni</i>	6.8 - 270.0	14.5 - 92.7	36.5	88
<i>Hydraena melas</i>	19.8 - 41.9			2
<i>Hydraena palustris</i>	6.8 - 355.0	17.1 - 130.0	60.7	45
<i>Hydraena pygmaea</i>	19.6			1
<i>Hydraena riparia</i>	7.1 - 534.0	18.8 - 172.2	64.4	174
<i>Hydraena testacea</i>	6.9 - 492.4	16.6 - 126.3	49.2	151

eastern, southern and northern parts of the country and between the large rivers and *H. britteni* is mainly found on the sandy soils in the southern, central and eastern part of the country.

CO-EXISTENCE

In table 5 the co-existence of five *Hydraena* species in The Netherlands is shown. The number of co-existences for each species exceeds the total number of occurrences because more than two species often co-exist. *H. assimilis* is found alone or in company with *H. testacea*. *H. britteni* lives most often alone or in co-existence with *H. testacea*. *H. palustris* lives most often in company with *H. riparia* and/or *H. testacea*, and only occasionally alone. *H. riparia* occurs most often alone, very frequently with *H. testacea* and frequently with *H. palustris*. *H. testacea* most often lives alone, very frequently with *H. riparia* and frequently with *H. britteni* and/or *H. palustris*.

Proportionally *H. britteni* is most often the only *Hydraena* species at a locality, indicating that its habitat requirements may be more exclusive than those of the other *Hydraena* species. *H. palustris* rarely occurs alone, and it shares its habitat quite often with *H. riparia* and/or *H. testacea*. *H. testacea*, though frequently occurring alone, co-exists quite often with all other *Hydraena* species, indicating that it can live in quite different habitats. *H. testacea* can be considered as the most euryoecious *Hydraena* species in The Netherlands.

Table 5. Association of *Hydraena* species in The Netherlands. N is the number of observations.

	N	Alone	with <i>H. assimilis</i>	with <i>H. britteni</i>	with <i>H. palustris</i>	with <i>H. riparia</i>	with <i>H. testacea</i>
<i>Hydraena assimilis</i>	10	4	—	2	—	1	6
<i>Hydraena britteni</i>	104	78	2	—	3	5	21
<i>Hydraena palustris</i>	52	11	—	3	—	28	19
<i>Hydraena riparia</i>	196	126	1	5	28	—	51
<i>Hydraena testacea</i>	164	82	6	21	19	51	—

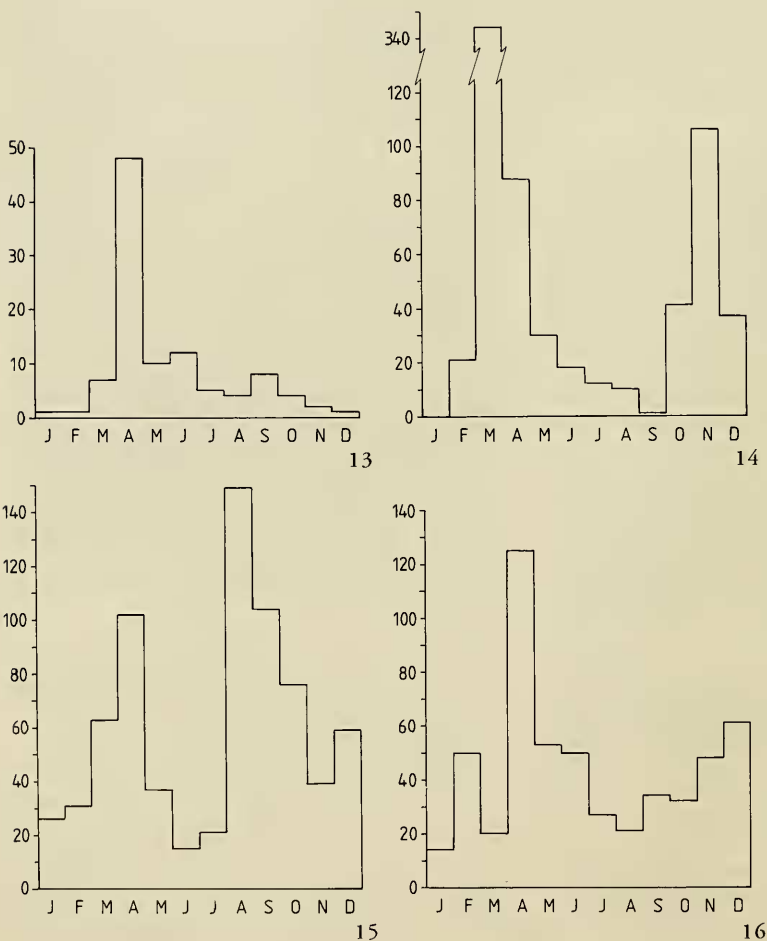
PHENOLOGY

Phenological data at monthly intervals of adult *Hydraena* species are given for *H. palustris*, *H. britteni*, *H. riparia* and *H. testacea* (figs. 13-16). For the remaining species the number of records of adults is too low to present meaningful diagrams. Keys for the identification of the larvae of *Hydraena* are not available and the larvae of only very few *Hydraena* species have been described so far (Hrbáček, 1943-44). As the number of collected larvae of this genus is very low and the above mentioned species quite often co-exist, it is impossible to include these data in the figures.

H. palustris has been collected throughout the year with a distinct maximum in April, which probably coincides with the breeding period. Cuppen (1983) reports a different phenology for *H. palustris* with a spring maximum in May and a (lower) autumn maximum in October.

The same phenology was found by Landin (1976) in Lake Sagsjön near Stockholm, though the autumn peak occurred in September. Adults in copula, however, have never been observed. Teneral adults have been observed between 7.viii and 18.xi, indicating a rather long emergence period, and without a clear autumn maximum. This type of life cycle agrees with life cycle type I of Nilsson (1986).

H. britteni can be collected throughout the year with clear maxima in March/April and November (the absence of records in January is certainly artificial). A similar phenology has been reported by Cuppen (1983) in a study of a population of *H. britteni* in a seepage-marsh near Apeldoorn (The Netherlands) during one year. Landin (1976) found a spring maximum in the beginning of May and a (lower) autumn maximum in September. The spring maximum coincides with the breeding period as many adults in copula have been observed between



Figs. 13-16. Number of specimens *Hydraena* species at monthly intervals. — 13, *Hydraena palustris* Erichson; 14, *Hydraena britteni* Joy; 15, *Hydraena riparia* Kugelann; 16, *Hydraena testacea* Curtis.

28.xii and 10.iv and the species can be considered as a winter breeder. Some pairs in copula even have been found in ice-covered pools. Teneral adults have been found in a very few occasions between 30.vii and 13.x before the November maximum. Cuppen (1983) mentions teneral adults in October and November. This low number of observations of teneral adults can be explained by the drying out of most habitats of *H. britteni* in the summer period. Adults probably leave their pupal chambers after the rising of the water level due to autumn rains, when they are already fully developed. The November maximum coincides with the filling up with water of the habitats of *H. britteni* during the period in which their gonads develop. This type of life cycle with winterbreeding is not mentioned by Nilsson (1986).

H. riparia has been collected throughout the year with two peaks in abundance in April and August/October. The spring maximum probably coincides with the breeding period but pairs in copula have been found only once on 4.iii. Teneral adults have been observed in great numbers between 23.vii and 13.xi (mainly August and the beginning of September), and therefore coinciding with the late summer maximum. The life cycle agrees with the life cycle type I of Nilsson (1986).

H. testacea has been collected quite evenly throughout the year with a maximum in April. This April maximum probably coincides with the breeding period though pairs in copula never have been found. Teneral adults have been found in abundance between 24.vii and 14.xi with a distinct maximum in September. Also in this species its life cycle is in agreement with type I of Nilsson (1986).

Based on the museum material, all other species have been collected mainly between May and September indicating more the activity of the collectors than the activity of the beetles. This also applies to the data for the above-mentioned species in the museum collections. The low number of records of *Hydraena* in museum collections is certainly partly based on the low activity of collectors in autumn, winter and spring.

DISCUSSION

The various distribution patterns of *Hydraena* in The Netherlands are in the first place determined by stream-velocity or a parameter associated with it. Most species are rheophilic or rheobiontic and therefore confined to the southern and eastern part of The Netherlands. The maps suggest that nearly all species of this group are restricted to areas with fast running waters and do not occur in areas with more slowly running lowland streams. Paucity of recent records of these species permits no further conclusions about

their preferred habitats. As running water species of *Hydraena* have no obvious morphological adaptations to that type of habitat it is difficult to judge which parameters are responsible for their restricted occurrence. A permanent high oxygen content of the water could be a main factor, as most species disappeared after pollution and subsequent decrease of oxygen.

For the stagnant water species chlorinity seems to be an important parameter for the explanation of their distribution patterns. All species are mainly restricted to waters with a chlorinity less than 200 mg/l. Other, less well known parameters, as soil type or the occurrence of seepage, probably also play an important role in their distributions. Quite often, however, two or three species can co-exist in the same locality, indicating that the different distribution patterns are not governed by the measured parameters.

Until 1991 twelve species of the genus *Hydraena* have been found in The Netherlands. Most of them, if not all, have been collected before 1950, but many of them were not recognized until recently after dissection of the male genitalia. From these twelve species only eight can be considered to occur at present in The Netherlands. *H. pulchella*, *H. minutissima*, *H. gracilis* and *H. belgica* have been collected for the last time at the beginning of this century and probably these species were confined to large streams as the Geul, Gulp, Voer (and Ratumse Beek) in the southern (and eastern) part of the country. Their disappearance is probably due to water pollution and, to a minor extent, to regulation of streams. Some of these species can, after improvement of water quality, return to The Netherlands from neighbouring streams in Belgium and Germany. However, colonisation power of *Hydraena* species seems to be limited. The remaining running water species (*H. melas*, *H. excisa*, *H. assimilis* and *H. pygmaea*) are all very rare and under serious threat. Especially *H. excisa*, which occupies an extreme western outpost in The Netherlands, will not easily return after extinction. The chances for survival of the other three species, which occur mainly in smaller streams or ditches receiving seepage-water, seem to be better, as most localities are situated in nature reserves. *Hydraena* species of stagnant waters are widely distributed and are not under threat. However, a decline of *H. testacea* and *H. riparia* in the western parts of The Netherlands is suggested by the available data.

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